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THE LIFE HISTORY OF *RELIQUIA SANTAMARTA*, A NEOTROPICAL ALPINE PIERINE BUTTERFLY (LEPIDOPTERA: PIERIDAE)

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Abstract.—Shapiro, Arthur M., Department of Zoology, University of California, Davis, California 95616.—The egg, larva, and pupa of *Reliquia santamarta* from the alpine zone of the Sierra Nevada de Santa Marta, Colombia are described. Resemblances to and differences from the early stages of the Nearctic *Pieris callidice* group are noted. Overall *R. santamarta* shows considerable differentiation from its alleged Nearctic relatives, but the hypothesis that it represents a relict of the stock which initially invaded South America from the north and subsequently underwent great adaptive radiation remains tenable.

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Reliquia santamarta Ackery is an unusual Pierine butterfly of uncertain affinities. It is known only from above 3,500 m in the Sierra Nevada de Santa Marta of northeastern Colombia, an isolated non-Andean range on the Caribbean margin. Discovered by Michael Adams in 1971, *R. santamarta* has been seen alive by only a handful of biologists. In January 1977 I was able to obtain fertile ova from 8 wild females collected at the type locality, the headwaters of the Rio Cambirumeina at 3,900–4,400 m. This material was reared at Cali, Colombia for use in photoperiod experiments which are being reported elsewhere (Shapiro, 1977a). Like the entire montane and alpine Neotropical Pierine fauna, *R. santamarta* has never been reported as reared in captivity.

The adult of *R. santamarta* is morphologically and phenotypically very similar to the Holarctic *Pieris callidice* Hubner group, which includes the familiar Nearctic *P. protodice* Bdv. & LeC. and *P. occidentalis* Reak. It is less similar to the widespread high Andean taxa of the genera *Tatochila*, *Phulia*, *Piercolias*, etc. and differs strikingly from them in having the submarginal lozenge-markings pointed basad in the interspaces, in this regard resembling true *Pieris*. The affinities of *R. santamarta* pose a critical problem for the interpretation of Pierine phylogeny and biogeography. It is generally assumed (Klots, 1933; Forster, 1958; Mani, 1968; Field and Herrera, 1977) that the entire Andean Pierine fauna evolved from a *Pieris*-type ancestor which invaded South America from the north in the Pliocene or Pleistocene, more or less in tandem with Andean orogeny. The same history is postulated for the Cruciferae, the plant family with which Pierini are predominantly associated globally (Raven and Axelrod, 1974:629). The

Sierra Nevada de Santa Marta is the northernmost mountain mass on the continent, and is characterized by an unusually high floral and faunal endemism (Adams, 1973, 1975). One of its oddest residents is the Pierid (Coliadini) *Nathalis iole* Bdv., which occurs in the high montane and alpine zones but is otherwise unknown in South America. It is a common "weedy" butterfly of dry, open sites in the southern and southwestern United States, in Mexico and northern Central America, and in parts of the West Indies. Because *N. iole* is so morphologically odd, possessing several characters normally associated with boreo-alpine Pierids, it has seemed "out of place" in its North American range. These traits, along with its oddly-shaped pupa, do not seem aberrant in its Colombian range and suggest daring new biogeographic hypotheses. The occurrence of *R. santamarta* in this range is exceptionally interesting in that this seems the logical place to look for a relict population of a northern invader, and the adult looks to "fill the bill." Neither Ackery (1975) nor Shapiro (1977a, b) was, however, able to pronounce on the relationships of *R. santamarta* with great confidence, given the lack of information on its early stages. These are now available for study.

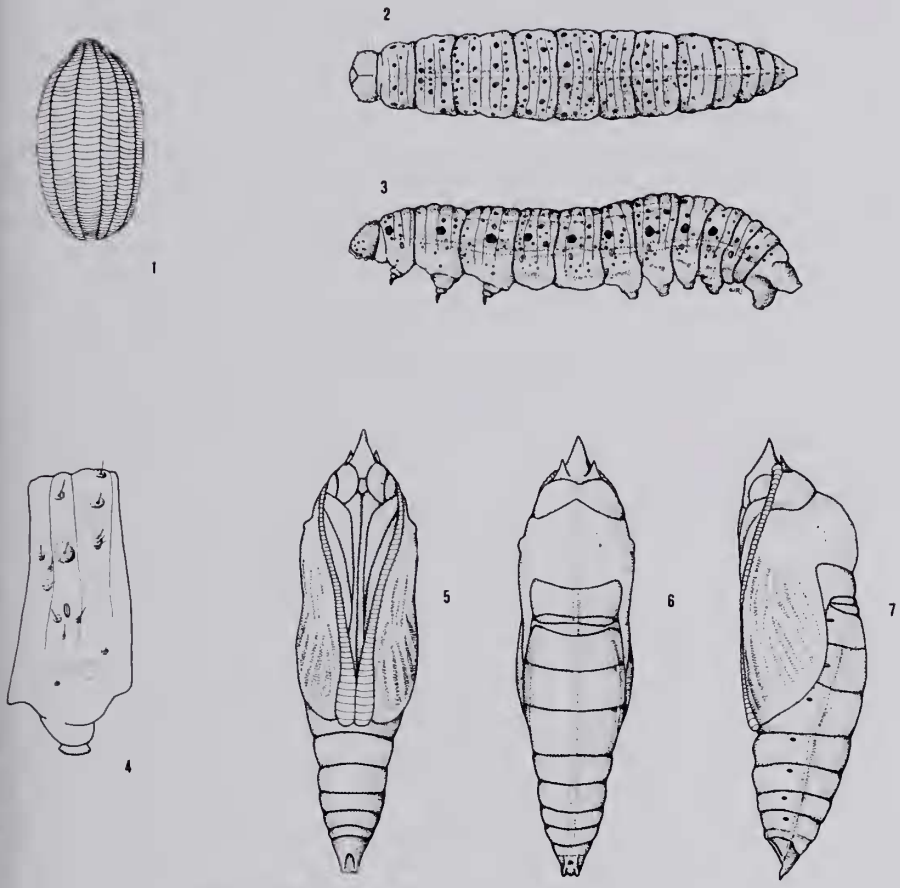
Rearing Procedures

These are described in more detail in Shapiro (1977a). Rearing was carried out at 26.5°C ± 2° on continuous light on fresh cuttings of the Cruciferous weed *Lepidium virginicum* L. from a vacant lot in Cali. This regime is very different from the conditions in which this species develops afield (Shapiro, 1977b). Since the adult phenotype was not modified (Shapiro, 1977a) it seems likely the early stages were also normal. The growth rate was certainly tremendously increased, very closely matching those of other high-altitude and -latitude Pierines reared at temperatures of 20°C or higher.

The descriptions which follow were prepared from live material and (fifth-instar larva, pupa, and egg) preserved specimens. Alcoholic material will be deposited with the British Museum (Natural History), the United States National Museum, and the Allyn Museum of Entomology, all of which have substantial adult series.

Descriptions

Egg (Fig. 1).—Size and form of the egg of *Pieris protodice*, 0.85 × 0.25 mm, erect, spindle-shaped, the chorion sculptured as figured, with about 12 vertical ribs; laid singly (in captivity—none were found afield) on leaves of various wild Crucifers. When laid dull yellow, changing within a few hours to orange-yellow and within two days to brick red; becoming blackish and translucent about 12 h before hatching. Time to hatch 6 days.



Figs. 1–7. *Reliquia santamarta* from northeastern Colombia. 1, egg, ×22.5. 2, mature larva, dorsal view. 3, mature larva, lateral view. 4, lateral view of seventh segment, showing major tubercles. 5, pupa, ventral view. 6, pupa, dorsal view. 7, pupa, lateral view. All ×3 except 4, ×15.

Larva: first instar.—At hateh 1 mm long; pale unmarked yellow with a dark head; usually eating the eggshell. After feeding on the leaf beeoming grayish green, unmarked, finely downy; head blaek. Begins as a pit feeder on leaves, soon switching to strip feeding. Length of instar 1½ days.

Second instar.—After molt 3.5 mm long at rest. Yellowish green, unmarked, finely downy, head blaek. By the end of the instar faint stigmatal yellow lines are visible, and a traee of a mid-dorsal one. Length of instar 1½ days.

Third instar.—After molt 7.5 mm long at rest. Gray-green; a faint yellow

mid-dorsal and stronger yellow stigmatal lines, these lines all bordered by conspicuous black tubercles of two sizes, with many very small less conspicuous tubercles scattered over the body at large; head at first gray-green, turning to dull brownish, mottled with black; ocelli black. Length of instar 2–3 days.

Fourth instar.—After molt 11 mm long. Ground color olivaceous gray-green; dorsal stripe pale yellow; stigmatal lines vaguely reddish yellow; black tubercles in three sizes, mostly bearing short black hairs. True legs black; venter and prolegs pale gray-green. Length of instar 2–3 days.

Fifth instar.—After molt 15 mm long at rest. Maximum resting size before prepupal period, 22 mm. Color as in fourth instar; by the Kornerup and Wanscher system (1967) ground color 3E6 ("olive"). Tuberculation as in Figs. 2–4. The last one or two fecal pellets produced before pupation are red, as in the *Pieris callidice* group. Before pupation the larva is very active and wanders for several hours prior to selecting a final site. Length of instar 3½–4 days.

Prepupa.—Similar to the *P. callidice* group. Attached by the anal legs and by a girdle around the thorax. Generally vertical, head up. Length of prepupal period, 8–12 hours. The prepupa does not become very pale in color, as occurs in *Euchloe ausonides* Lucas of the Nearctic which has a somewhat similar larva.

Pupa (Figs. 5–7).—Length 18 mm, width at girdle 4.7 mm. After pupation bright green (27A6), usually but not always changing within 24 h to light buff (4A2, "yellowish white"), pattern as shown, with indistinct dark markings between the wing-veins (5D4, "light brown"); in color very similar to dormant pupae of *Pieris napi* L. rather than to members of the *callidice* group, which are characteristically grayish. Frontal prominence short, as in the *callidice* group, much shorter than in any *napi* population. The two supraocular prominences larger than in the *callidice* group or any Holarctic *Pieris*, approaching the frontal one in size. Most strikingly, the flaring dorsolateral prominences (near the outer angles of the wing cases), which are moderately developed in the *callidice* group and greatly so in *P. rapae* L. and *P. napi*, are entirely absent. The shape of the pupa suggests a *Colias*, but with uninflated wing cases. Before emergence the eyes, wings, and body are pigmented in that order, with white pigment laid down in the wings several hours before black. Meconium red, as in the *P. callidice* group. Length of pupal period, 6–7 days.

Discussion

The early stages of *Reliquia santamarta* are perplexing. There are strong hints of relationship to the *Pieris callidice* group in all stages. The egg is virtually identical, the larval striping and tuberculation are somewhat

similar, the pupa has a similar facies except for the lack of dorsolateral prominences, and—perhaps most significantly—the larval wastes before pupation and the meconium are both red, a trait shared only with the *callidice* group among the Nearctic Pierines. There are, however, so many aberrant traits that one must hesitate before accepting a close kinship. The ground color of the mature larva is unlike any Nearctic Picrine; it most closely approaches *Pieris beckeri* Edwards. However, it is identical to the color of larvae of *Pieris brassicae* L. of Palaearctic, and it shares with that species the three-stripe pattern, along with a pronounced but hard-to-define "oily" look. Unlike *P. brassicae* the larvae are not gregarious and do not stink. The pupa also somewhat resembles *P. brassicae* in having a small frontal prominence, but the enlargement of the supraoculars is similar to the condition in the Andean genus *Tatochila* (Shapiro, 1977c) and points to a connection there—otherwise resemblances in the early stages are minimal. The first and second instar larvae are reminscent of *Pieris sisymbrii* Bdv., but the later instars are not. *P. sisymbrii* has a blue-green egg of an unusual shape and an aposematically-colored fifth-instar larva which loses all its tubercles, and despite its facies does not seem to be closely related to the *callidice* group.

In culture *R. santamarta* behaved as a leaf, rather than an inflorescence, feeder when presented with *Lepidium* tops. In the Nearctic, leaf-feeding Pierines tend to have cryptic green larvae with faint dorsal and stigmatal yellow stripes, while inflorescence feeders are striped lengthwise in purplish-gray and yellow. These patterns have evolved independently in closely related species pairs in *Pieris* (Pierini) and also in *Euchloe* (Euchloini). This suggests that although the larva of *R. santamarta* has not been found in the wild, it is probably a foliage feeder on the perennial rosette Crucifers (many gray-green) which abound in its rocky alpine habitat.

The geologic interpretation of the Caribbean margin, including the Sierra Nevada de Santa Marta, is in flux and in any case exceedingly complex (Tschanz et al., 1974). Several hypotheses can be advanced to account for the range of *R. santamarta*, but given the various resemblances to the *P. callidice* group (including such "offbeat" characters as egg and meconium color) and the link to *Tatochila* in pupal shape, the most persuasive hypothesis is the traditional one which makes the Andean Pierines derivative from Nearctic invaders and assigns to *Reliquia* a truly relict status. *R. santamarta*, it should be noted in passing, has well-developed androconia while these have been lost by *P. protodice*, *callidice*, and *occidentalis*. It also has the long antennae characteristic of the Andean *Hypsochila* and *Pierphulia* and some lowland Neotropical genera, e.g. *Itaballia*. There are definite hints that if the Nearctic-invasion hypothesis is correct, the ancestor of *R. santamarta* was a more primitive Pierine than

the present-day *callidice* group, whose distribution demonstrates a pre-Pleistocene origin.

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Literature Cited

Ackery, P. H. 1975. A new Pierine genus and species, with notes on the genus *Tatochila* (Lepidoptera: Pieridae). Bull. Allyn. Mus. 30:1–9.

Adams, M. 1973. Ecological zonation and the butterflies of the Sierra Nevada de Santa Marta, Colombia. J. Nat. Hist. 7:699–718.

———. 1975. Full report of the "Third North Colombia Butterflies Expedition, 1974/75." Privately circulated mimeograph. 42 pp.

Field, W. D., and J. Herrera. 1977. The Pierid butterflies of the genera *Hypsochila* Ureta, *Phulia* Herrich-Schäffer, *Infraphulia* Field, *Pierphulia* Field, and *Piercolias* Staudinger. Smithson. Contrib. Zool. 232:1–64.

Forster, W. 1958. Die Tiergeographischen Verhaltnisse Boliviens. Proc. X Internat. Congr. Entomol. 1956, 1:843–846.

Klots, A. B. 1933. A generic revision of the Pieridae (Lepidoptera), together with a study of the male genitalia. Entomol. Amer. 12:139–242.

Kornerup, A., and J. H. Wanscher. 1967. Methuen Handbook of Colour. London: Methuen. 243 pp.

Mani, M. S. 1968. Ecology and Biogeography of High-Altitude Insects. The Hague: W. Junk. 527 pp.

Raven, P. H., and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Mo. Bot. Gard. 61:539–673.

Shapiro, A. M. 1977a. Evidence for obligate monophenism in *Reliquia santamarta*, a Neotropical alpine Pierine butterfly. (Ms under review.)

———. 1977b. Notes on the behavior and ecology of *Reliquia santamarta*, an alpine butterfly (Lepidoptera: Pieridae) from the Sierra Nevada de Santa Marta, Colombia, with comparisons to Nearctic alpine Pierini. Stud. Neotrop. Fauna Envt., in press.

———. 1977c. The life history of an equatorial montane butterfly, *Tatochila xanthodice* (Lepidoptera: Pieridae). (MS under review.)

Tschanz, C. M., et al. 1974. Geologic evolution of the Sierra Nevada de Santa Marta, northeastern Colombia. Bull. Geol. Soc. Amer. 85:273–284.